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Characteristics of different populations of the gudgeon (*Gobio gobio* L.) in Flanders, Belgium

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ABSTRACT. We examined the possible effects of isolation on population characteristics of the gudgeon, *Gobio gobio* L., 1758. Isolated populations appeared to have significantly lower densities than non-isolated populations. Length-frequency distributions showed that most non-isolated populations had a healthy composition, with a larger number of young animals, and a smaller number of older animals. However, for some isolated populations this was not the case, despite the fact that some of them had high densities. Four condition factors were compared between isolated and non-isolated populations. They showed no relationship with isolation, although significant differences among populations were found. Fluctuating asymmetry (FA) was determined using metric and meristic traits. The meristic traits could not detect the presence of FA, but the metric traits showed that FA was present in some populations. Significant differences were found among populations, but the FA could not be related to isolation. The growth rate showed significant differences among populations, but was not related with isolation. The maximum swimming speed, oxygen consumption, ammonia production, and ammonium quotient were assessed in the laboratory. None of these parameters showed a relationship with isolation, but there were significant differences among populations. Overall, our results show that population density and distribution seem to be affected by isolation, while for the other parameters no effects of isolation were found. However, significant differences among populations were found for all other parameters.

KEY WORDS: gudgeon, isolation, condition, population structure, fluctuating asymmetry, swimming capacity, oxygen consumption, ammonia excretion.

INTRODUCTION

Destruction and fragmentation of natural habitats by man is the major reason for the worldwide decrease in biodiversity (Quinn & Harrison, 1988). While the adverse effects of anthropogenic habitat fragmentation are well documented for most native terrestrial plants and animals, its importance as an isolating mechanism in stream-dwelling species has been largely overlooked (Dodd, 1990). However, the natural area of most Flemish fish species, such as the gudgeon (*Gobio gobio* L., 1758), is often highly fragmented by the presence of barriers (e.g. dams, weirs, water mills, pumping-engines, pollution) (Utzinger et al., 1998), leading to the isolation of populations. In many species, the population size will decrease due to isolation, making these populations more vulnerable to extinction (Soulé, 1983; Stefann-Dewenter & Tscharntke, 1999). A possible explanation for this decrease could be that some species are no longer able to find all of their resources (food, spawning area, shelter,..) in the reduced habitat (Spellerberg, 1996). Another consequence of isolation is that the exchange of individuals and genetic material between populations might decrease (Lande, 1988; Lande & Barrowclough, 1990). Especially in small populations, this will lead to the depletion of genetic variation (i.e. genetic erosion). In isolated populations, inbreeding will increase as population size decreases, resulting in a reduced fitness (inbreeding depression) and in heterozygosity loss (Allendorf, 1983; Lande & Barrowclough, 1990). Several studies have demonstrated a reduced body weight and volume, a lower fitness and a lower fecundity in isolated populations compared to non-isolated populations (Lande & Barrowclough, 1990; Wauters et al., 1996; Wiggins et al., 1998; Tanaka, 2000). The lower body weight and volume could have a negative influence on the physiological condition of the animals (Wauters et al., 1996). For

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instance, fishes with a lower body weight might have less energy reserves and/or a lower swimming capacity. Condition factors, derived from the length-weight relationship, are often used as bio-indicators for environmental stress, and are thought to be related to fitness (Lambert & Dutil, 1997; Dutil et al., 1998; Suneetha et al., 1999). A lower condition might influence the tolerance of fishes to an additional stress, such as lower oxygen concentrations. Furthermore, a reduced heterozygosity might result in a higher fluctuating asymmetry (FA) (i.e. the random deviations from perfect symmetry in bilaterally paired traits) (Leary & Allendorf, 1989; Palmer, 1994).

We examined the possible effects of isolation on the population characteristics of the gudgeon, by: (1) comparing condition factors and growth rates between isolated and non-isolated populations, (2) studying the effects of isolation on the population structure, and (3) studying the effect of isolation on physiological parameters that could be related to condition (e.g. swimming capacity, oxygen consumption and ammonia production).

MATERIAL AND METHODS

Sampling

We sampled sites with a comparable water quality, throughout Flanders (Fig. 1), using electrofishing. Sites were considered to be isolated if there were any obstructions (higher than 15 cm) or a strong pollution present downstream from the site. Information about water quality was obtained from the online database of the Dutch Environmental Company (http://www.vmm.be). The sites were sampled from 22/10/99 to 28/02/00 to investigate the population structure. From 25/02/99 to 16/03/00 four isolated and five non-isolated sites (both with high gudgeon densities) were sampled to obtain fish for the laboratory study.

Test species

The gudgeon (*Gobio gobio*) belongs to the family of the cyprinids and is widespread in European rivers. It was selected as test species for several reasons. First of all gudgeons are abundant and widespread in the Flemish water courses (Vandelannoote et al., 1998), implying that sampling would not endanger its survival. Secondly, since gudgeons have a limited home range, individuals caught at a specific site can be considered to be representative for the selected sampling site (Stott, 1967; Stott et al., 1963). Thirdly, gudgeons have not been introduced in the selected study area.

Field study

During each sampling session, we used depletion fishing to estimate population size. At each site, three subsequent captures were performed, and the fish caught during each capture were kept separately in plastic tanks. Population size was then calculated according to two methods: the method of DeLury, as described by Laurent & Lamarque (1975), and the method of Zippin, as described by Southwood (1968). The fork length of the fish was measured to the nearest mm, and the weight was measured to a precision of 0.1 g, using an electronic balance (KERN 442-43). Based on the length-weight relationship, four condition factors were calculated (Weatherly, 1972; Bagenal, 1978). This relationship followed the equation: $W = a * FL^b$ [1] (with W = weight and FL = fork length).

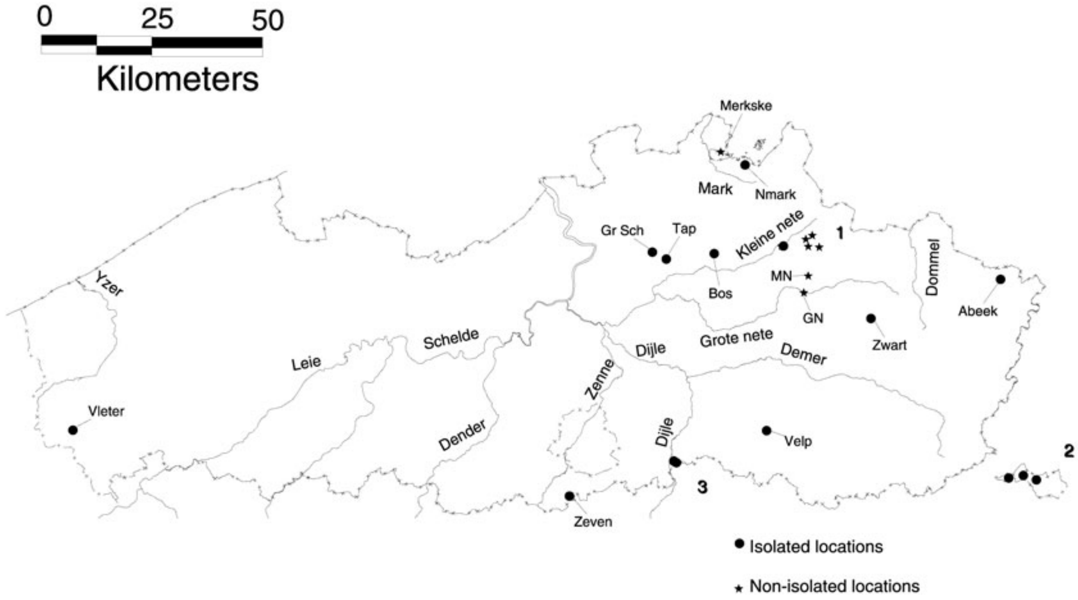

Fig. 1. – Sampling sites for gudgeon in Flanders. Used abbreviations: Nmark = Noordermark, MN = Molse Nete, Gr Sch = Groot Schijn, Tap = Tappelbeek, GN = Grote Nete, Vleter = Vleterbeek, Zwart = Zwarte Beek, Zeven = Zevenborrebeek.

Fulton's condition factor (FULTON) was calculated by the formula: $K = (100*W)/FL^3$. Two adapted condition factors were calculated by $K' = (100*W)/FL^b$ (b as the value calculated in equation [1]). The first adapted condition factor (ADCF 1) was calculated using the b-value for each population separately, while the second one (ADCF 2) was calculated using the overall b-value. The relative condition factor from Le Cren (LECREN) was calculated by: $K'' = W/W^{exp}$; W^{exp} being the weight of the fish as expected based on equation [1].

From each gudgeon, six scales were taken from above the lateral line (left side). These scales were dried for at least three days, then washed in a 0.1 N NaOH solution, and finally they were mounted on a microscopic slide. The annual rings on the scales were counted using a microprojector (Heerbrug Projectina type 4002). This allowed us to determine the age, from which the growth was subsequently calculated using the 'back calculation' method of Fraser-Lee (Bagenal, 1978). The relationship between fork length (FL) and scale radius (SR) follows the equation: FL = a+b*SR [2]. From this relationship, the fork length at a given age n (FL_n) can be calculated by the formula:

$$FL_n = \frac{AR_n}{SR} * (FL - a) + a$$

in which AR_n is the distance between the centre of the scale and the n-th annual ring, and a is the intercept from equation [2].

Fluctuating asymmetry (FA) was studied by examining both metric and meristic bilateral traits. The meristic traits were counted in the field: (SCAL); the number of scales above the lateral line, and (PELVRAY); the number of rays counted at the base of the pelvic fin. The metric traits were the height (H) and the width (W) of the fourth scale along the lateral line, counted from head to tail. For these traits, the left and right side were measured repeatedly (sequence left-right-left-right) to the nearest 0.1 mm, using a microprojector (Heerbrug projectina type 4002). Repeated measurements were necessary to distinguish true FA from measurement error (Lens et al., 1999).

Small fin clips were taken from all gudgeons for further DNA-analysis (during this study, the primers for gudgeon DNA were not yet available).

Laboratory study

Four isolated and five non-isolated locations were studied. From each location, seven gudgeons, ranging in size from 6-13 cm, were taken to the lab and acclimated for three days at a temperature of 15° C, and at a photoperiod of 10 h light/ 14 h darkness.

The first two days of the acclimation period, fish were fed with midge larvae.

All experiments were carried out in seven respirometers (Fig. 2), analogous with the Blazka-respirometer (Beamish et al., 1989).

To determine the critical swimming speed, seven fish were measured and weighed as described before, and then placed in the respirometers. The respirometers were connected to a continuous flow system to ensure sufficient oxygen concentrations. The front side of each respirometer was covered with a black plastic, in order to minimize the disturbance caused by the observer. After these preparations, the fish were left alone for an hour to allow them to calm down. Then a water current of 10 cm/s was applied. Every 20 minutes, the velocity was raised by 5 cm/s (Keen & Farrell, 1994; Lauff & wood, 1996; Alsop & Wood, 1997). When a fish became exhausted, it was pushed against the back membrane. When this happened, the current was lowered for a few seconds and then reinstalled to its original velocity. If the fish was pushed against the membrane a second time, the experiment was stopped and the time and velocity of the occurrence were noted. The critical swimming speed (U_{crit}) was then calculated as follows (Keen & farrell, 1994; Lauff & wood, 1996; Alsop & wood, 1997; McDonald et al., 1998):

$$U_{crit} = U_p + \left(\frac{T}{t}\right) + dU$$

With U_p as the last velocity at which the fish was able to swim during a complete time interval, T = the time the fish swam during the velocity of exhaustion, and t = time interval (20 minutes), dU = speed increment (5 cm/s). The critical swimming speed was then expressed in units of body length/s.

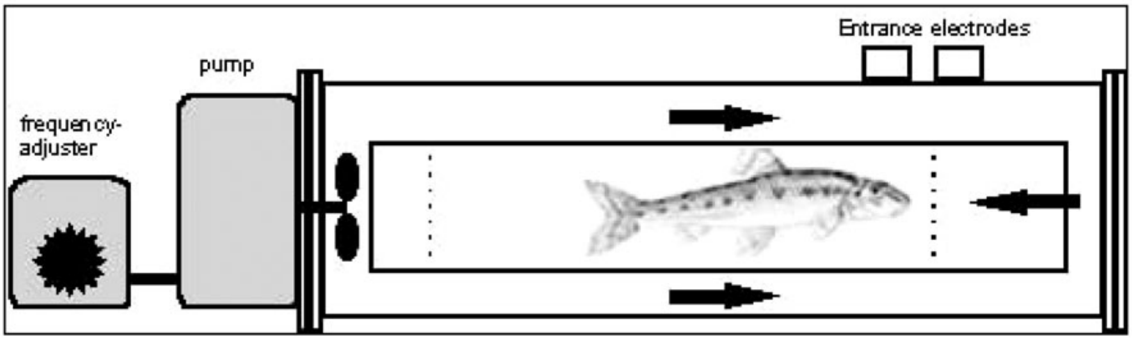

Fig. 2. – Schematic figure of the respirometer. The black arrows indicate water flow, the dotted lines represent membranes, which keep the fish in the inner tube and allow water to flow through the inner tube.

The day after determination of the critical swimming speed, oxygen consumption and ammonia excretion were measured. For this, the fish used in the previous experiment were held in the respirometers over night, with the respirometers connected to a continuous flow system. For each population, one fish was removed, so that there was one respirometer for the blanco measurements. The fish were forced to swim at a velocity equal to $^1/_4$ of U_{crit} for two hours. During this experiment, the respirometers were closed so that no atmospheric oxygen could enter the system. Oxygen concentrations were continuously measured using WTW CellOx 325 electrodes, which were connected to a computer for automatic reporting (WINDMILL 4.06 software). At the beginning and the end of each experiment, 4 ml water samples were taken in triplicate to measure total ammonia concentration. This measurement was done using the hypochlorite-phenol method (Grasshoff, 1976). After the experiments, FA and growth were determined for the tested fishes as described above.

Statistical analysis

Normal distribution of data was tested using the Kolmogorov-Smirnov test, and homogeneity of variance was tested using the Bartlett test (Zarr, 1996; Dytham, 1999). If both assumptions were fulfilled, one-way ANOVA was performed to check for differences among locations, followed by a Tukey-Kramer test. If one of these assumptions was not fulfilled, a non-parametric test (Kruskall-Wallis test for differences among populations and Mann-Whitney-U test for differences between isolated and non-isolated populations), followed by a post hoc Dunn's test, was used. Correlations were tested with Spearman-rank correlation. All these tests were performed in Graphpad Instat® 3.01. The analysis of FA was performed using the mixed procedure in SAS, in which individuals were defined as repeated statement. Restricted maximum likelihood (REML) test was used to distinguish true FA from measurement error (Lens & Van Dongen, 1999). An F-test was used to distinguish FA from directional asymmetry.

RESULTS

Field study

Using the method of Delury and the method of Zippin, very similar results were obtained. Population densities (Fig. 3) were significantly higher in non-isolated than in isolated populations (Mann-Whitney U, P = 0.0098). This was still the case if the site 'Witte Nete', with an exceptionally high population density (807 ind./100 m), was not included in the analysis (P = 0.022). This clearly shows that the population density is affected by isolation. While nine of the fifteen isolated locations had population densities lower than 30 individuals per 100 m, there was only one of the eight non-isolated locations with such a low density.

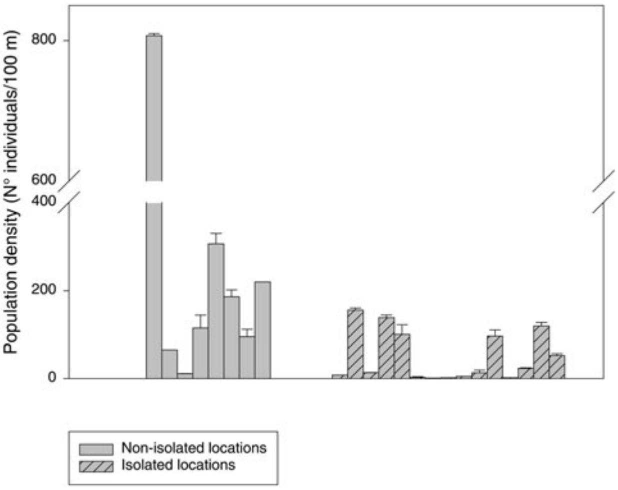

Fig. 3. – Population densities for the gudgeon. Dashed bars represent isolated populations. Densities are expressed as number of individuals/ 100 m.

Length-frequency distributions are given in Figs 4a-4b. For three isolated locations the length-frequency distribution is not shown, because at each location only few gudgeons were caught (Nethen 1: 1 gudgeon, fork length 106 mm; Nethen 2: 1 gudgeon, fork length 139 mm and Voer: 2 gudgeons, fork lengths 122 and 134 mm). Obviously, populations with small individual numbers have a very narrow distribution of length classes, consisting mainly of larger and older fish. These populations are all isolated populations. Furthermore, only two isolated locations with a population density larger than 30 individuals per 100 m show a population structure that consists of a relatively large number of young (small) individuals, and a smaller number of larger (older) individuals (i.e. Abeek and Noordermark). The other isolated high density populations have a larger number of older individuals compared to young individuals (i.e. Vleterbeek, Berwijn, Groot Schijn and Velp). For the non-isolated populations, a population distribution with a relatively large number of young animals was found in all cases, even for the one location with a low density (i.e. Desselse Nete point 1).

The meristic traits could not be used to detect FA; for both traits (SCAL and PELVRAY), deviations from the normal bilateral symmetry were only found in two fishes. However, the metric traits (H and W) allowed us to detect FA. The real asymmetry was always significantly larger than measurement error (REML test, all P-values < 0.001). The average values of the assigned asymmetry were never significantly different from zero (F-test, all P > 0.1), meaning that the asymmetry was due to FA and not to directional asymmetry. For both traits, there were significant differences (KW, P < 0.0001) in FA among populations (Figs 5a-5b), but these differences could not be related to isolation due to insufficient data for the non-isolated populations (due to lack of time, we were only able to obtain data for the site 'Witte Nete').

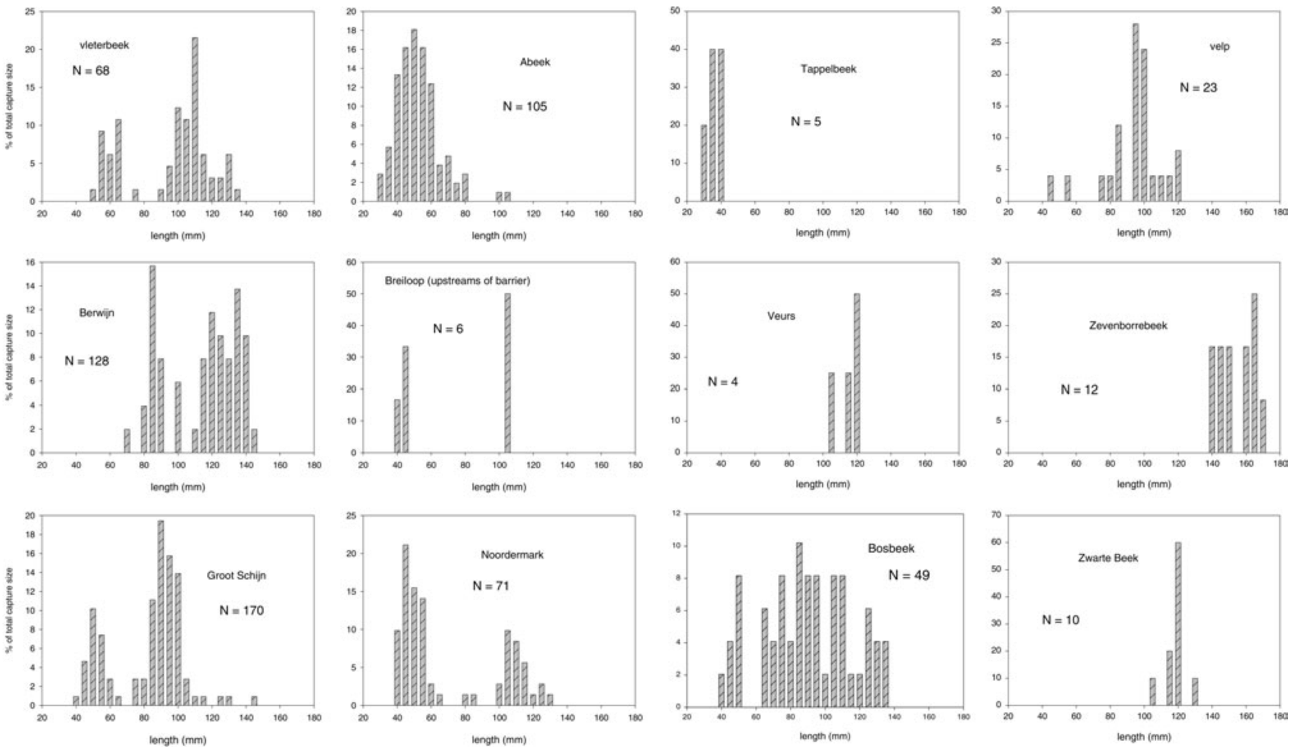

Fig. 4a. – Length-frequency distributions for isolated populations of the gudgeon. N is the total number of fish caught at the site during the sampling; length intervals are taken at 5 mm.

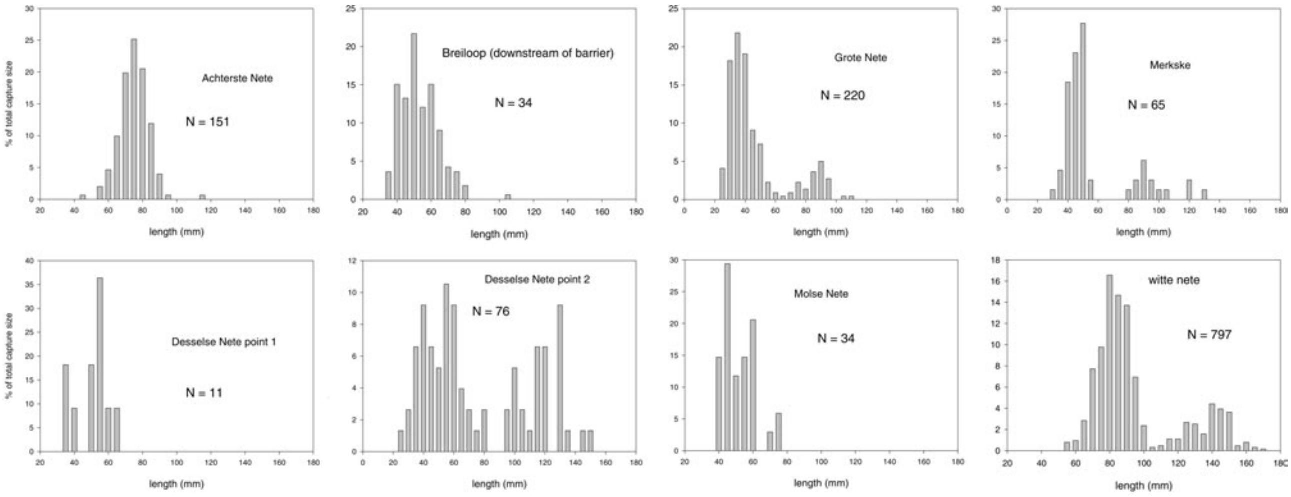

Fig. 4b. – Length-frequency distributions for non-isolated populations of the gudgeon. N is the total number of fish caught at the site during the sampling; length intervals are taken at 5 mm.

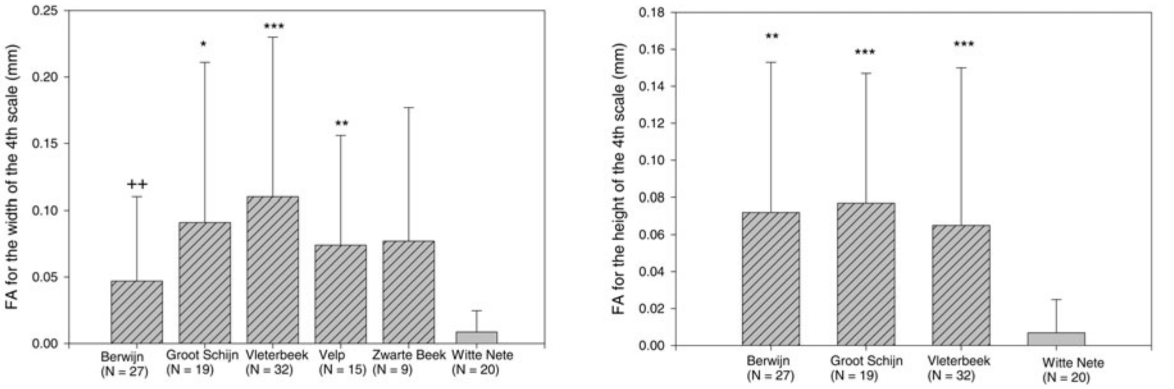

Fig. 5. – *a*. (left). Means and standard deviations of the fluctuating asymmetry for trait W. *b*. (right). Means and standard deviations of the fluctuating asymmetry for trait H. Dashed bars represent isolated populations. ++: significantly lower FA than Vleterbeek ($P < 0.01$); *: significantly higher FA than Witte Nete (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

The back-calculated fork lengths showed a linear relationship with age, allowing us to determine growth rates by linear regression. The growth rates (Fig. 6) differed significantly among populations (ANCOVA, ddfm = 4 and 1162, F = 36.37, P < 0.001), but could not be related to isolation (Table 1).

For the calculation of the condition factor of Fulton (FULTON), the data were divided into five length classes (<60 mm, 60-80 mm, 80-100 mm, 100-120 mm and > 120 mm). For all length classes, the results were similar. A Kruskall-Wallis ANOVA showed that there were significant differences among populations (for each length class : P < 0.01), and a Dunn's post hoc test showed that the FULTON-value was significantly higher for one isolated population (i.e. Vleterbeek) (Table 2), but the condition factor of Fulton could not be related to isolation.

There were also significant differences among populations for the adapted condition factors (i.e. ADCF 1 and 2) (for both: P < 0.001), but neither one of these condition factors could be related to isolation. For both of the adapted condition factors, the Vleterbeek population had the highest condition, but there were also significant differences among the other populations (Table 3).

Similar results were found for the condition factor of Lecren (LECREN): there were significant differences among populations (P < 0.001), but they could not be related to isolation. The LECREN value was also the highest for the Vleterbeek population.

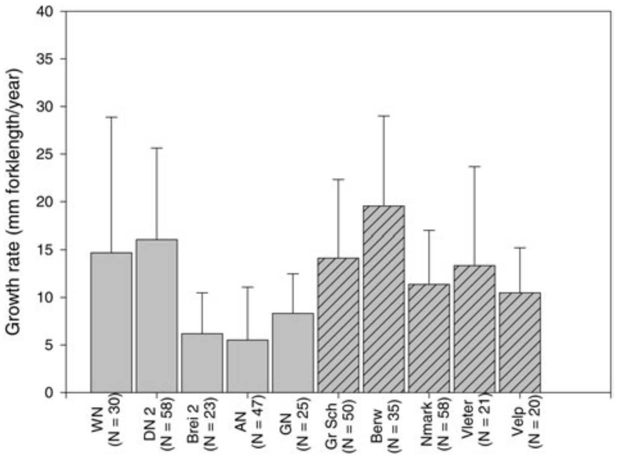

Fig. 6. – Means and standard deviations of the growth rates (in mm fork length/year) for gudgeon populations. Dashed bars represent isolated populations. N = number of fishes used to determine age and growth.

TABLE 1

Differences in growth rate among populations. ns: not significant; *: P < 0.05; **: P < 0.01; ***: P < 0.001. ^{i}: isolated populations.

	WN	**DN 2**	**Brei 2**	**AN**	**GN**	**Gr Sch^{i}**	**Berwijn^{i}**	**Nmark^{i}**	**Vleter^{i}**	**Velp^{i}**
WN	---									
DN 2	ns	---								
Brei 2	***	***	---							
AN	***	***	ns	---						
GN	***	ns	ns	ns	---					
Gr Sch^{i}	ns	ns	***	***	***	---				
Berwijn^{i}	***	*	***	***	***	***	---			
Nmark^{i}	ns	***	***	***	ns	ns	***	---		
Vleter^{i}	ns	ns	***	***	**	ns	***	ns	---	
Velp^{i}	*	***	*	***	ns	*	***	ns	ns	---

TABLE 2

Results of the Dunn's multiple comparisons test for FULTON, for the length class < 60 mm. The results for the other length classes are similar. ^{i}: isolated populations. ns: not significant; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

	Desselse Nete	**Merkske**	**Molse Nete**	**Achterste Nete**	**Breiloop 2**	**Grote Nete**	**Noordermark^{i}**	**Groot Schijn^{i}**	**Abeek^{i}**	**Vleterbeek^{i}**
Desselse Nete	---									
Merkske	ns	---								
Molse Nete	ns	ns	---							
Achterste Nete	ns	ns	ns	---						
Breiloop 2	ns	ns	ns	ns	---					
Grote Nete	ns	ns	ns	ns	ns	---				
Noordermark^{i}	ns	ns	ns	ns	ns	ns	---			
Groot Schijn^{i}	ns	ns	ns	ns	ns	ns	ns	---		
Abeek^{i}	*	ns	ns	ns	ns	ns	ns	ns	---	
Vleterbeek^{i}	***	***	**	*	***	***	***	**	**	---

TABLE 3

Results of the Dunn's multiple comparisons test for ADCF 1. The results for the ADCF 2 are similar. ^{i}: isolated populations. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

	Witte Nete	**Desselse Nete**	**Velp^{I}**	**Abeek^{i}**	**Groot Schijn^{i}**	**Achterste Nete**	**Berwijn^{i}**	**Grote Nete**	**Breiloop 2**	**Molse Nete**	**Merkske**	**Noordermark^{i}**	**Vleter^{i}**
Witte Nete	---												
Desselse Nete	***	---											
Velp^{i}	ns	***	---										
Abeek^{i}	***	***	***	---									
Groot Schijn^{i}	***	ns	***	**	---								
Achterste Nete	ns	***	ns	***	***	---							
Berwijn^{i}	***	***	***	ns	*	***	---						
Grote Nete	***	***	***	ns	**	***	ns	---					
Breiloop 2	***	ns	***	***	ns	***	***	***	---				
Molse Nete	ns	***	***	***	***	ns	***	***	***	---			
Merkske	***	ns	***	***	ns	***	***	***	ns	***	---		
Noordermark^{i}	ns	*	***	***	***	***	***	***	*	***	ns	---	
Vleter^{i}	***	***	***	***	***	***	***	***	***	ns	***	***	---

Laboratory study

The results for the critical swimming speed are shown in Table 4. Significant differences were found among populations ($P < 0.01$), and the Dunn's multiple comparisons test showed that the populations from Velp (isolated) ($P < 0.01$) and from Witte Nete (non-isolated) ($P < 0.05$) had lower mean critical swimming speeds than the population from Groot Schijn (isolated). Therefore, the critical swimming speed did not seem to be related to isolation.

The oxygen consumption (Table 5) also was not related to isolation, although significant differences were found among populations ($P = 0.007$). The populations from Merkske (non-isolated) ($P = 0.006$), Groot Schijn (isolated) ($P = 0.006$) and Achterste Nete (non-isolated) ($P = 0.004$) had higher oxygen consumptions than the population from Velp (isolated). Also, the populations from Merkske (isolated) ($P = 0.02$), Groot Schijn (isolated) ($P = 0.02$) and Achterste Nete (not-isolated) ($P = 0.03$) had higher oxygen consumptions than the Abeek population (isolated).

There were significant differences among populations for the ammonia production (P = 0.0001), but the ammonia production (Table 6) was also not related to isolation.

TABLE 4

Means and standard deviations of the critical swimming speed (U_{cr}), in body lengths/s. ^{i}: isolated populations. For each population, N = 7.

Population	**Critical swimming speed**	
	Mean	Stdev
Velp^i	2.99	1.15
Abeek^i	5.48	1.54
Groot Schijn^i	6.98	0.65
Bosbeek^i	6.19	2.03
Witte Nete	3.62	1.22
Merkske	5.66	0.89
Achterste Nete	6.72	2.03
Desselse Nete 1	4.58	1.86
Desselse Nete 2	4.09	2.06

TABLE 5

Means and standard deviations of the oxygen consumption, in umole*g^{-1}*h^{-1}. ^{i}: isolated populations. For each population, N = 6.

Population	**Oxygen consumption**	
	Mean	Stdev
Velp^i	6.29	1.13
Abeek^i	4.95	2.55
Groot Schijn^i	13.60	7.68
Bosbeek^i	11.65	4.60
Witte Nete	9.65	7.00
Merkske	13.60	7.68
Achterste Nete	12.25	6.28
Desselse Nete 1	7.64	3.12
Desselse Nete 2	7.38	1.78

TABLE 6

Means and standard deviations of the ammonia excretion, in umole*g^{-1}*h^{-1}. ^{i}: isolated populations. For each population, N = 6.

Population	**Oxygen consumption**	
	Mean	Stdev
Velp^i	0.27	0.09
Abeek^i	0.21	0.12
Groot Schijn^i	0.50	0.19
Bosbeek^i	0.34	0.10
Witte Nete	0.45	0.19
Merkske	0.36	0.10
Achterste Nete	0.55	0.14
Desselse Nete 1	0.26	0.07
Desselse Nete 2	0.24	0.13

Correlations

None of the condition factors was correlated with the physiological parameters from the laboratory study, nor with the FA (all P > 0.05). The FA, the oxygen consumption and the critical swimming speed were not related with any of the other parameters (all P > 0.05).

DISCUSSION

Field study

Population densities were higher in non-isolated than in isolated populations. Perhaps, this could partially be explained by the width of the selected sites: most of the isolated sites were smaller than the non-isolated sites. However, the range of widths was rather small (2-8 m), and in broader rivers, electrofishing becomes less efficient, potentially leading to an underestimation of the population size. Another explanation for the difference in population size could be given by adverse effects of isolation. Inbreeding depression, demographic stochasticity and environmental stochasticity are possible causes for a decline in population size (LANDE, 1988; WIGGINS et al., 1998).

For the estimation of the population densities, two different methods were used. The results from both methods were very similar, but the method of Zippin allowed us to calculate the standard error as well, while the method of DeLury did not. Although LAURENT & LAMARQUE (1975) claim that the DeLury method may be used to calculate standard errors, it is not statistically correct, as the X and Y values used to make the estimate are not independent of each other (SOUTHWOOD, 1966). Standard errors are required to perform statistical analysis, so it is preferable to use the method of Zippin.

A healthy population structure consists of a relative large number of small fish and a small number of larger fish (NIKOLSKII, 1980; SCHLOSSER, 1982; MATTHEWS, 1998). While for all non-isolated populations a healthy population structure was found, this was only the case in two isolated populations. This suggests that isolation affects the population structure and density. Maybe individuals from the non-isolated populations have a higher reproductive success, or they suffer less from genetic erosion than the isolated populations. Future DNA-analyses of fin clips will allow us to examine whether there are genetic differences between isolated and non-isolated populations.

The meristic traits could not detect the presence of FA in this study. The use of meristic traits in FA-analysis has the disadvantage that they result in integer values. This means that FA will not be detected using only meristic traits, unless the amount of FA is very large, which only occurs in very extreme conditions (AMES et al., 1979; PALMER, 1994). However, the metric traits showed that FA was present in some populations. Significant differences were found among populations, but the FA could not be related to isolation due to insufficient data for the non-isolated populations. Nevertheless, the fact that we were able to detect the presence of FA in some populations, might indicate that FA is a useful tool for studying effects of isolation.

No relationship was found between isolation and growth rate. The highest growth rate was found for an isolated water course, the Berwijn, which might be explained by the high productivity (food availability) of this river (Bervoets, unpublished data). Possible effects of isolation on the growth rate might be shaded by effects of other environmental influences, such as food availability, temperature, flow regime, etc… The effects of sex on growth were not investigated in this study, but Lobon-Cervia et al. (1991) demonstrated that gender has little or no influence on the growth rate of the gudgeon.

Condition factors have been linked to survival of fish (Booth & Hixon, 1999). For all condition factors, significant differences were found among populations. This might indicate ecological differences among the populations, since condition factors are thought to be related to the fitness of fish. However, none of the condition factors was related to isolation. The condition factor of Fulton reached lower values in this study (values ranging from 0.8 to 1.4) than in the study of Lobon-Cervia et al. (1991) (values ranging from 1.0 to 1.6). This might be explained by the warmer climate in Spain.

Laboratory study

The critical swimming speed showed no relation with isolation. However, we should emphasize that significant differences among populations were present. A possible complementary parameter for the swimming speed is the swimming activity (i.e. the time the fish actually swim during a given period). Similar results were found for the oxygen consumption and ammonia excretion. The swimming performance is related to survival (escaping from predators, searching for food) and to reproductive success (reaching suitable spawning areas, finding a mate) (Keen & farrell, 1994; Lauff & wood, 1996; Alsop & wood, 1997; McDonald et al., 1998). Therefore, differences in critical swimming speed may have implications for the fitness of fish. Oxygen consumption and ammonia excretion are often used as endpoints in toxicity tests, and have proven to be very sensitive measures for stress (Kutty, 1972; De Boeck et al., 1995). The oxygen consumption values found in this study lie within the same range found for other cyprinids (5-15 μmole.g^{-1}.hour^{-1}) (Forstner & Wieser, 1989). De Boeck et al. (1995) found ammonium excretions for carp up to 0.7 μmole.g^{-1}.hour^{-1}, which is also comparable with those found for gudgeon in this study.

All three physiological parameters have ecological relevance. The fact that for the three physiological parameters, significant differences were found among populations, might be an indication that there are ecological differences among these populations. It is possible that food availability has an important influence on these parameters, but unfortunately we did not measure food abundance.

Conclusions

Population density and structure were the only population characteristics that were affected by isolation. This could make isolated populations even more vulnerable to extinction through demographic and/or genetic and/or environmental processes. For the other population characteristics, we could not detect clear differences between isolated and non-isolated populations. However, there were significant differences among populations for all other parameters.

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